Fossorial origin of the turtle shell

Lyson, Tyler R ; Rubidge, Bruce S ; Scheyer, Torsten M ; de Queiroz, Kevin ; Schachner, Emma R ; Smith, Roger M H ; Botha-Brink, Jennifer ; Bever, G S

Abstract: The turtle shell is a complex structure that currently serves a largely protective function in this iconically slow-moving group [1]. Developmental [2, 3] and fossil [4-7] data indicate that one of the first steps toward the shelled body plan was broadening of the ribs (approximately 50 my before the completed shell [5]). Broadened ribs alone provide little protection [8] and confer significant locomotory [9, 10] and respiratory [9, 11] costs. They increase thoracic rigidity [8], which decreases speed of locomotion due to shortened stride length [10], and they inhibit effective costal ventilation [9, 11]. New fossil material of the oldest hypothesized stem turtle, Eunotosaurus africanus [12] (260 mya) [13, 14] from the Karoo Basin of South Africa, indicates the initiation of rib broadening was an adaptive response to fossoriality. Similar to extant fossorial taxa [8], the broad ribs of Eunotosaurus provide an intrinsically stable base on which to operate a powerful forelimb digging mechanism. Numerous fossorial correlates [15-17] are expressed throughout Eunotosaurus' skeleton. Most of these features are widely distributed along the turtle stem and into the crown clade, indicating the common ancestor of Eunotosaurus and modern turtles possessed a body plan significantly influenced by digging. The adaptations related to fossoriality likely facilitated movement of stem turtles into aquatic environments early in the groups' evolutionary history, and this ecology may have played an important role in stem turtles surviving the Permian/Triassic extinction event.

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Report

Current Biology

Fossorial Origin of the Turtle Shell

Highlights

- Recently discovered stem turtles indicate the shell did not evolve for protection
- Adaptation related to digging was the initial impetus in the origin of the shell
- Digging adaptations facilitated the movement of turtles into aquatic environments
- Fossoriality likely helped stem turtles survive the Permian/Triassic extinction

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In Brief

The origin of the turtle shell is a major evolutionary transition whose initial function was unknown. Lyson et al. present a strongly supported idea that a burrowing ecology and adaptations related to digging favored the initial transformations on the road to the modern turtle shell. Only later was the shell coopted for protection.

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Report

Fossorial Origin of the Turtle Shell

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SUMMARY

The turtle shell is a complex structure that currently serves a largely protective function in this iconically slow-moving group [1]. Developmental [2, 3] and fossil [4–7] data indicate that one of the first steps toward the shelled body plan was broadening of the ribs (approximately 50 my before the completed shell [5]). Broadened ribs alone provide little protection [8] and confer significant locomotory [9, 10] and respiratory [9, 11] costs. They increase thoracic rigidity [8], which decreases speed of locomotion due to shortened stride length [10], and they inhibit effective costal ventilation [9, 11]. New fossil material of the oldest hypothesized stem turtle, *Eunotosaurus africanus* [12] (260 mya) [13, 14] from the Karoo Basin of South Africa, indicates the initiation of rib broadening was an adaptive response to fossoriality. Similar to extant fossorial taxa [8], the broad ribs of *Eunotosaurus* provide an intrinsically stable base on which to operate a powerful forelimb digging mechanism. Numerous fossorial correlates [15–17] are expressed throughout *Eunotosaurus*' skeleton. Most of these features are widely distributed along the turtle stem and into the crown clade, indicating the common ancestor of *Eunotosaurus* and modern turtles possessed a body plan significantly influenced by digging. The adaptations related to fossoriality likely facilitated movement of stem turtles into aquatic environments early in the groups' evolutionary history, and this ecology may have played an important role in stem turtles surviving the Permian/Triassic extinction event.

RESULTS

Adaptation to their environment plays an important role in shaping the morphology of organisms. The selective regime of specific ecologies often results in the convergent evolution of derived morphologies in different anatomical regions among phylogenetically distant groups (e.g., flippers and fusiform shape of aquatic leatherback turtles, cetaceans, ichthyosaurs, and mosasaurs). By examining the context in which a trait evolved, one can evaluate alternative hypotheses regarding its function [18]. Such analyses are crucial to understanding how adaptations can change through time to shape simple elements into complex structures. A classic example is the evolution of feathers from simple, unbranched structures accepted as playing a role in sexual selection or thermoregulation in early stem birds (i.e., dinosaurs) to complex flight feathers in modern birds [19].

The turtle shell is an evolutionary novelty, but unlike the rich fossil record of feathers, the deep history of the turtle shell is not as well documented. The scarcity of critical fossils bridging the morphological gap between the ancestral amniote body plan and the highly modified body plan of turtles prevented insights into the original function and underlying environmental impetus for the origin of the shell. Only recently have partially shelled stem turtles been discovered [4], or rediscovered [5, 7, 11, 20], and integrated with developmental data [2, 21–24] to allow for the confident homologizing of the ~50 elements that make up the shell [25]. These data indicate that most of the carapace is made up of ribs and vertebrae that broaden via the outgrowth of intramembranous bone, and not via the fusion of the ribs and vertebrae with overlying osteoderms (e.g., [26, 27]). In addition, older fossil stem turtles with primitive shells have recently been identified [5–7], providing critical data on early stages in the assembly of the complex turtle shell [5] (Figure 1). The morphologies of these early stem turtles (sensu Bever et al. [7]), particularly the oldest one, *Eunotosaurus africanus* (260 million years ago [mya]), can now be placed in their

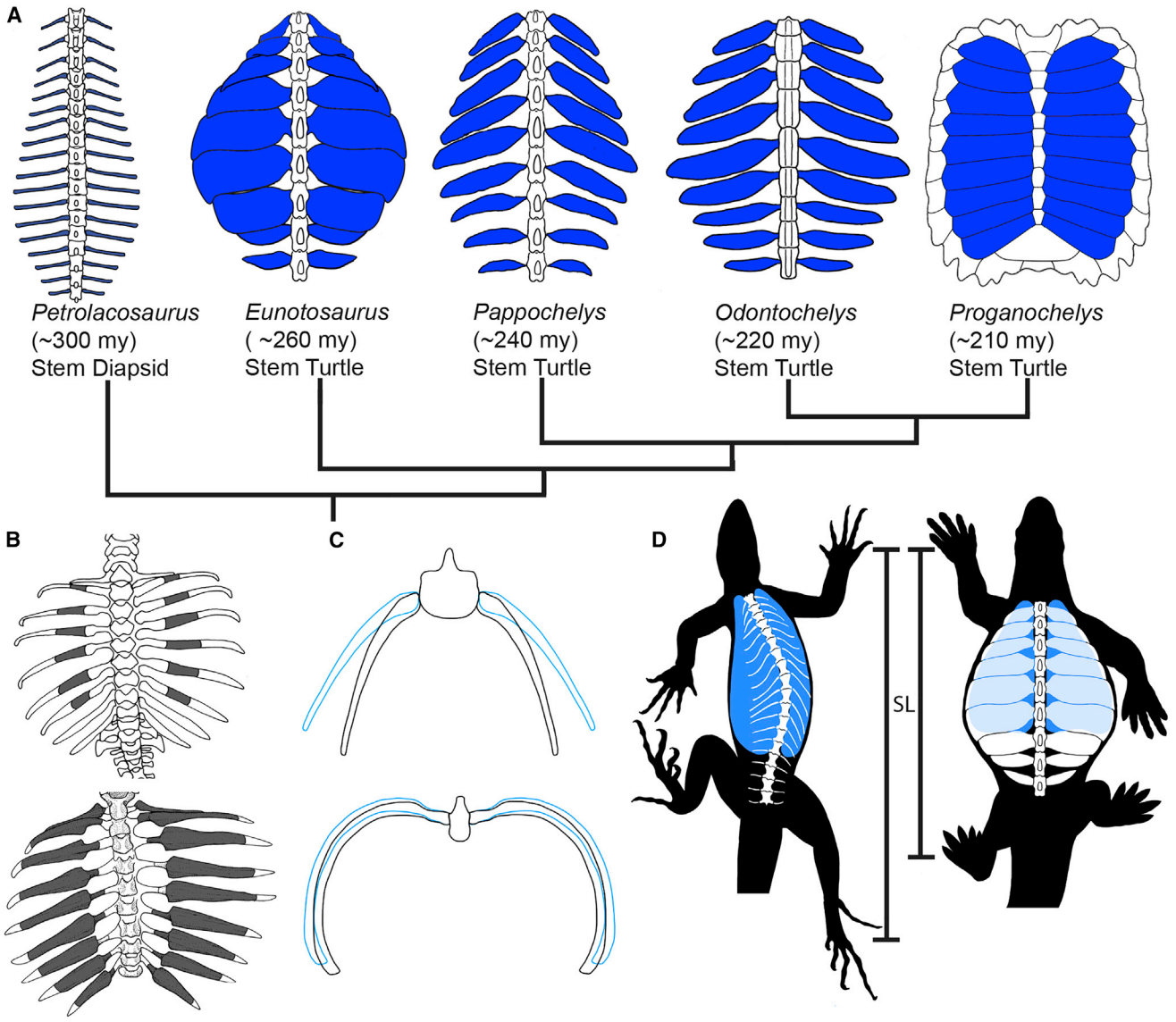


Figure 1. Evolution of the Turtle Shell and Its Associated Respiratory and Locomotory Constraints

One of the first major deviations from the ancestral amniote body plan, both phylogenetically [4–6] and developmentally [2, 3], is the appearance of anteroposteriorly broadened dorsal ribs, which entails significant respiratory and locomotory costs.

(A) The fossil record documents the evolutionary history of the craniocaudally broadened dorsal ribs (blue) and the beginnings of the shell in stem turtles.

(B) The development of the shell of *Chelydra serpentina* shows that the ossification (gray) and broadening of the ribs happens early in development, between stages 20 (top) and 23 (bottom) (illustrations modified from [3]).

(C) Comparison of the dorsal (blue) and ventral (black) movement of the dorsal ribs in cranial view indicates the broadened ribs found in the early stem turtles *Eunotosaurus* (bottom), *Pappochelys*, and *Odontochelys* are less effective costal ventilators compared to reptiles ancestrally (top) due to the mechanical conflict created by the broadened overlapping ribs [11].

(D) Ancestrally, lateral bending of the body helps to propel sprawling taxa (left; e.g., lepidosaurs, basal amniotes, etc.). Craniocaudally broadened ribs of stem turtles (right, *Eunotosaurus*) increases the rigidity of the body wall, which decreases bending and shortens the stride length (SL), significantly slowing sprawling taxa [9]. Blue represents lungs.

paleoenvironmental context, facilitating a rigorous test of the original function for the origin of the turtle shell.

In order to determine the original paleoecology of the turtle shell, our study analyzes new specimens of *Eunotosaurus* (Experimental Procedures), which provides novel morphological data (e.g., complete manus and pes, ulna, femur, etc.). In addition, we obtained new histological data from both forelimb and hindlimb elements (Experimental Procedures). All of these data are more broadly compared to those of extant animals (Table S1) and stem turtles crownward of *Eunotosaurus* (Table S2).

Respiratory and Locomotory Costs of Broadened Ribs

Both phylogenetically [5–7] and developmentally [2, 3], one of the first major deviations of turtles from the ancestral amniote body

plan is the appearance of anteroposteriorly broadened dorsal ribs (Figure 1). This change has significant respiratory and locomotory costs. Ancestrally, amniote ribs and their associated hypaxial muscles have a dual function of ventilating the lungs and stabilizing the flexible thoracic wall during sprawling, lateral-bending locomotion [9] (Figures 1C and 1D). Compared to other early amniotes, the ribs of the early stem turtles *Eunotosaurus africanus* (260 mya), *Pappochelys rosinea* (240 mya), and *Odontochelys semitestacea* (220 mya) are relatively ineffective costal ventilators owing to the mechanical conflict created by their broadened morphology [11]. This conflict has been considered important in moving from the dual function of ribs and hypaxial muscles in the ancestral amniote to a division of function in turtles where the expanded ribs (shell) support locomotion and the hypaxial muscles power ventilation of the lungs [11]. Broadened ribs and the reduction in vertebrae (from 18 to 9) and rib numbers in early stem turtles cause an increase in body wall rigidity [8, 11]. This also affects lateral-bending locomotion present in tetrapods with a sprawling gait, including most other early amniotes [10]. Sprawling early amniotes, as well as extant lepidosaurs, use lateral bending of the body wall to increase stride length and speed [9, 10]. The modified thoracic anatomy in early stem turtles increased body wall rigidity, shortened stride length, and decreased their speed [10]. Hence broadened ribs and overall increased thoracic rigidity in early stem turtles have consequences for both respiration and locomotion (Figure 1). For this specialized morphology to have evolved via natural selection, an adaptive advantage that outweighs these costs was required.

The current protective function (e.g., [1]) conferred by the shell in extant turtles fails to adequately explain the impetus for the initial broadening of the ribs in the early stem turtles *Eunotosaurus* and *Pappochelys*. In these animals, the head and neck remained unprotected, and much epaxial musculature was exposed between the dermis and bone, as in the case of extant mammals with similarly broadened ribs (see [8]). It is only later, in *Odontochelys*, that broadening of the vertebral neural spines provided some protection for the epaxial muscles [4, 5] (Figure 1). In addition, covering the body with osteoderms, a protective feature found in numerous amniote groups (pareiasaurs, ankylosaurid dinosaurs, cyamodontoid placodont reptiles, armadillos, various squamates, crocodylians, etc.), is less costly in terms of impact on both respiration and locomotion [8] than protection via broadened dorsal ribs.

A Case for Fossoriality in the Oldest Stem Turtle *Eunotosaurus africanus*

New fossil material of *Eunotosaurus* provides an alternative hypothesis for the origin of broadened ribs and the early history of the turtle shell. Osteological, including histological, correlates for fossoriality are found throughout its skeleton (Figure 2). The method of digging (e.g., humeral rotation, scratch, etc.), soil type, purpose of digging (e.g., food, shelter, etc.), and mode of locomotion (sprawling versus upright) determines where in the skeleton fossorial osteological correlates are located (Table S1) [8, 15]. In *Eunotosaurus*, such correlates are found in the skull, neck, thoracic cavity, and forelimb (Figure 2), indicating that these regions of the body played a significant role in their fossorial lifestyle. All fossorial animals, however, share the functional problem of leverage in that the digging stroke must displace substrate and not the body [8]. As in extant broad-ribbed taxa (e.g., giant anteater [8]), the broad ribs of *Eunotosaurus* would have provided a stable base on which to operate a powerful shoulder and forelimb digging mechanism, as well as bestowing additional stability to the vertebral column, which joins the digging forelimbs to the bracing, supporting hindlimbs. Overall, the suite of fossorial correlates is most similar to those found in other sprawling fossorial taxa such as the extant burrowing gopher tortoises (*Gopherus*) and the Early Triassic cynodont *Thrinaxodon* (Table S1), which has anteroposteriorly broadened ribs and is commonly found in fossilized burrows [28, 29].

Gopher tortoises use their head and neck to brace themselves against the burrow while digging with their forelimbs and have a number of derived features in these regions [30], all of which are also found in *Eunotosaurus*. The remarkable overlap in fossorial osteological correlates between *Gopherus* and *Eunotosaurus* (Table S1) supports a similar mode of digging. Both taxa have a short, spade-shaped skull (Figure 2) that is able to absorb and redistribute mechanical loads resulting from its use in digging [30]. The broadening of the occipital region (Figure 2) in both taxa increases both the area of attachment and the mechanical advantage of neck musculature (Figure S1) used to stabilize the cranio-cervical joint [30]. *Gopherus* and *Eunotosaurus* have short, robust cervical vertebrae with massive zygapophyses that are situated between the vertebral bodies and bulbous neural spines (Figures S1D and S1E), which indicate well-developed neck musculature. In addition, *Eunotosaurus* has long, deep cervical ribs that merge with the thoracic ribs to create a fusiform body [31] (Figure S1). As in *Gopherus* [30], these derived features aid in transferring the transverse bending force (produced when using the skull and neck to brace against the burrow to counteract the forelimb digging movements) from the cranio-cervical joint, and they spread it along the entire neck and anterior thoracic region (Figure S1G).

Adaptations related to a powerful shoulder and forelimb digging mechanism in *Eunotosaurus* include the following: a well-developed tubercle on the posterior coracoid for insertion of the triceps muscle [31]; presence of a large acromion process on the scapula [31]—the early origins of the tri-radiate shoulder girdle; a manus that is larger and more robust than the pes (Figure 3); a robust humerus with a well-developed deltopectoral crest; a short robust ulna with a well-developed olecranon process; a large manus with short non-terminal phalanges; and large spatula-shaped terminal phalanges that are longer than the penultimate phalanges (Figures 2 and 3). As in extant fossorial taxa [15], these osteological features are related to the additional muscular strength needed for flexing or extending the shoulder, elbow, and wrist while breaking up the soil. This enhanced strength is reflected in the histologic section of the ulna and humerus (Figure 2) where abundant Sharpey's fibers (ShFs) populate the areas of muscle attachment. In addition, the compact cortical wall of the ulna is exceptionally thick with a relative thickness of 40%, which is another correlate of fossoriality [16, 17] (Figure 2). While thick cortical bone walls and abundant ShFs are found in the ulna and humerus, they are absent in the hindlimbs (Figure 2). This important relationship indicates these histological features are related to the compressive forces [17] experienced by the digging forelimb and are not simply characteristics of the entire skeleton.

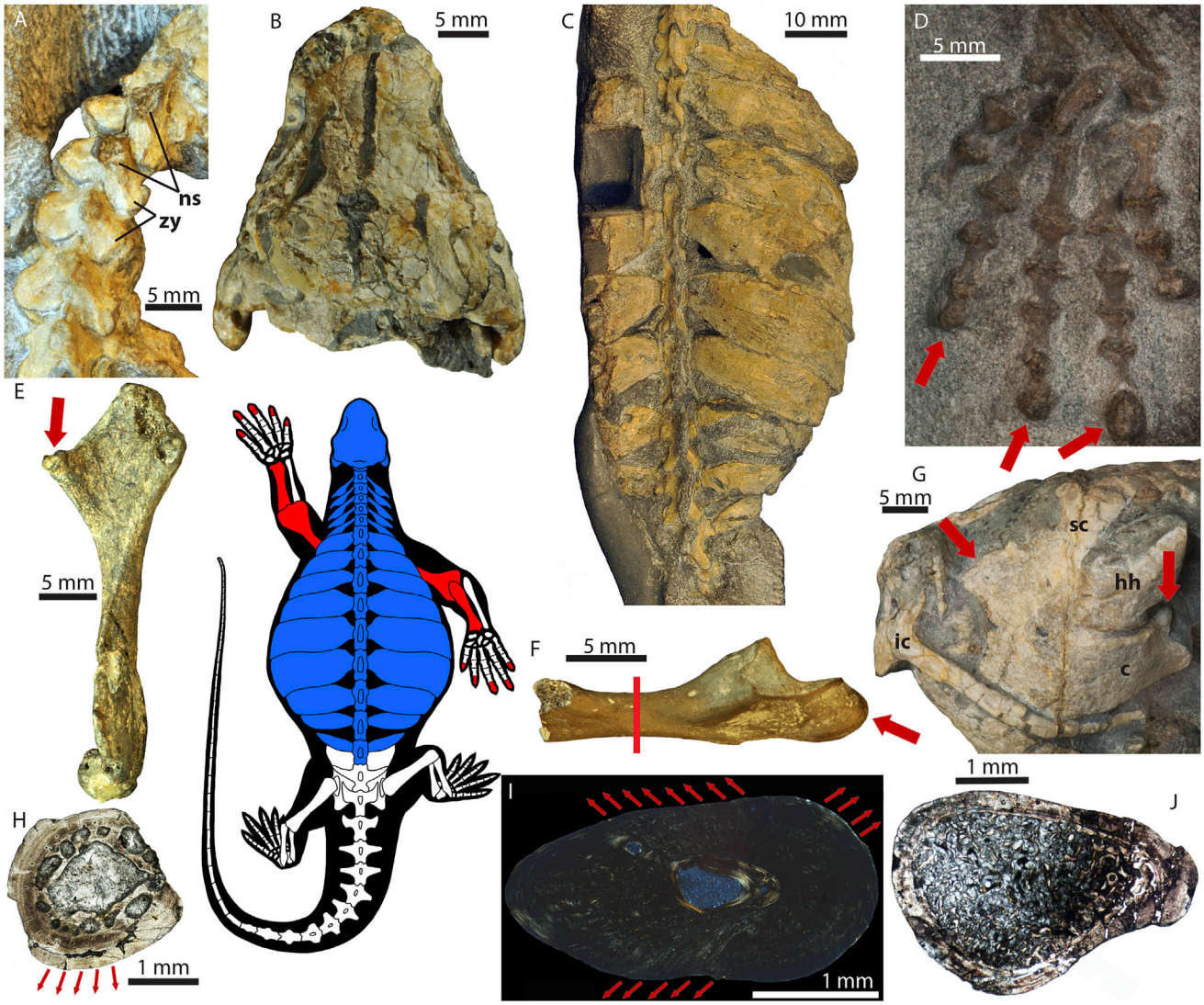


Figure 2. Osteological, Including Histological, Correlates for Fossoriality in *Eunotosaurus*

(A–C) Correlates related to counteracting the forces generated by the forelimb digging apparatus (blue in whole-body illustration) are expressed in the neck (A), skull (B), and thoracic region (C).

(A) Cervical vertebrae (CM 86-341) in dorsal view showing the short, robust cervical centra with bulbous neural spines (ns) and exceptionally massive zygapophyses (zy) that are situated between the vertebral bodies (also see Figure S1).

(B) Skull (CM777) in dorsal view showing the short, spade shape with a broaded occipital region and closure of the upper temporal fenestrae.

(C) Trunk region (CM 86-341) in dorsal view showing the anteroposteriorly broadened thoracic ribs.

(D–I) Correlates related to the digging mechanism (red in whole-body illustration) are found in the forelimb (D–F) and shoulder girdle (G).

(D) Large manus (FPM 2014/269) in ventral view showing the short non-terminal phalanges and the large spatula-shaped terminal phalanges (red arrows) that are longer than the penultimate phalanges.

(E) Right humerus (USNM 23009) in anterior view showing the well-developed deltopectoral crest (red arrow).

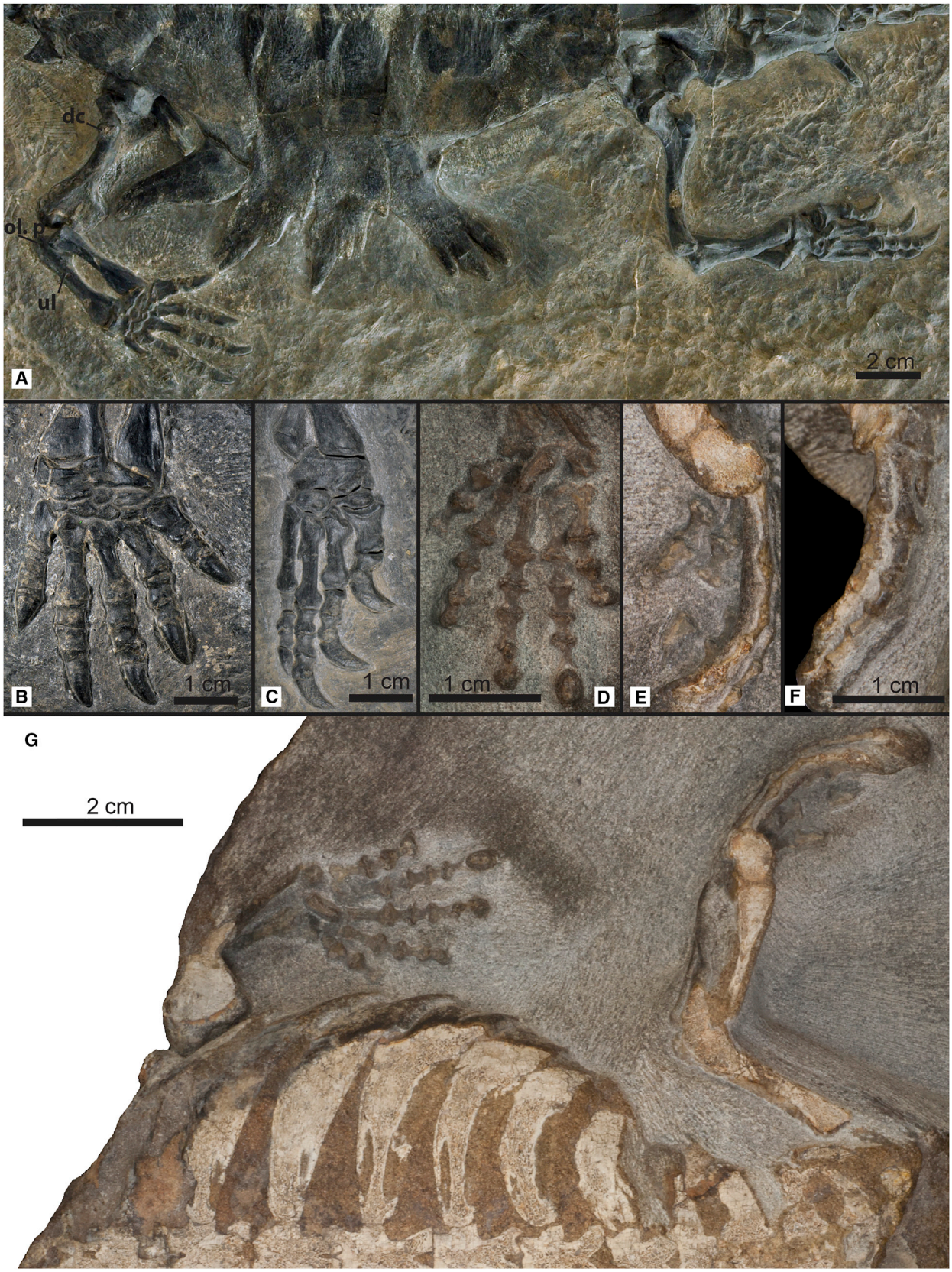
(F) Left ulna (USNM 23009) in ventral view showing the well-developed olecranon process (red arrow).

(G) Ventrolateral view of the left shoulder girdle (CM777) showing the presence of a large acromion process (red arrow) on the scapula (sc) and a well-developed tubercle (red arrow) on the coracoid (c) for insertion of the triceps muscle. hh, humeral head; ic, interclavicle.

(H–J) Histological section from the proximal diaphysis of a humerus from a juvenile specimen (H; CGP/1/3000) and midshaft section of an ulna from a presumed sub-adult specimen (I; USNM 23009) both with exceptionally thick bone walls (>40% of total width) and abundant Sharpey's Fibers (red arrows) dorsally and ventrally; both features are lacking in the histological section from the mid-shaft of the fibula from a sub-adult specimen (J; BP/1/7024).

See also Figure S1.

The rare preservation of complete sclerotic rings in a recently found skull of *Eunotosaurus* (Figure 4) provided us with an unexpected opportunity to estimate the overall size of the eye and its sensitivity to light [32–34]. The scleral ossicles in *Eunotosaurus* are not flat but rather form a concave cup over the eye (Figure 4B). It is not possible to determine the number of ossicles,



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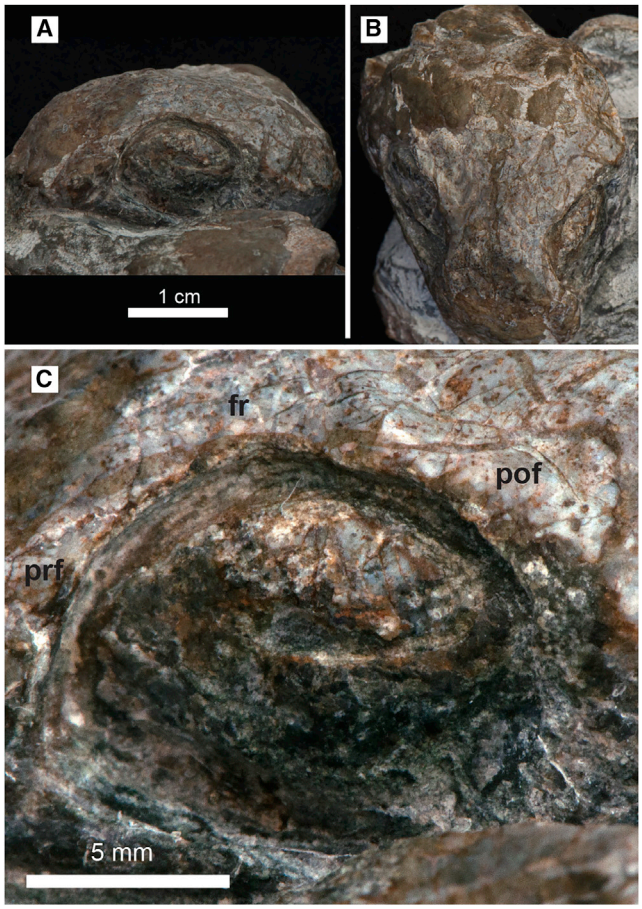

Figure 4. Morphology of the Eye in *Eunotosaurus africanus*

Scleral ossicles in the orbit of *Eunotosaurus* indicate it had relatively large, photopic (diurnal) eyes with low sensitivity to light.

(A) *Eunotosaurus* skull and scleral ossicles (SAM-PK-K11350) in left lateral view show the sclerotic ring (external diameter = 9.07 mm) largely fills the diameter of the orbit (orbit length = 10.51 mm), indicating an approximately 10 mm diameter for the eye.

(B) *Eunotosaurus* skull in dorsal view (scale bar same as in A) showing the cup-shaped morphology of the sclerotic ring.

(C) Close-up view of the left orbit showing the small, internal diameter (1.41 mm) of the scleral ring, indicating the diameter of the lens and iris was approximately 1.41 mm. fr, frontal; pof, postfrontal; prf, prefrontal.

but they largely fill the orbit. An orbit length (OL) of 10.51 mm and an external diameter of the sclerotic ring (EXT) of 9.07 mm indicate the diameter of the eye is approximately 10 mm. The internal diameter of the sclerotic ring (1.41 mm) indicates the diameter of the pupil and lens was approximately 1.41 mm. The optical ratio (INT^2/(OL × EXT) [33] is 0.0209. The optical ratio allows for an estimation of light sensitivity [33], and, compared to both extant and extinct amniotes [32–34], the sensitivity level is extremely low in *Eunotosaurus*. The ratio for *Eunotosaurus* indicates an eye with low sensitivity to light—a common feature among extant fossorial animals (e.g., *Gopherus*, amphisbaenians, caecilians, etc.; [15]). Unlike fossorial animals that are rarely above ground and therefore have very small eyes (e.g., caecilians, amphisbaenians, etc.; [15]), the comparatively large eyes (~10 mm) of *Eunotosaurus* are more similar to those of fossorial animals that dig burrows for shelter but habitually forage above ground (e.g., gopher tortoises).

DISCUSSION

The skeletal modifications related to providing a stable base and powerful forelimb digging mechanism, combined with the sensory fossorial correlates, indicate a burrowing lifestyle for the early stem turtle *Eunotosaurus*. Many of these osteological correlates of fossoriality are also found in stem and crown turtles (Table S2), supporting the hypothesis that fossoriality was not an autapomorphy of *Eunotosaurus* but rather played an important role in the early evolution of turtles. All other partially shelled stem turtles (sensu Bever et al. [7]) have anteroposteriorly broadened dorsal ribs, a robust humerus with a well-developed deltopectoral crest, and a scapula with a prominent acromion process. Many stem turtles have a well-developed olecranon process on a robust ulna (i.e., *Palaeochersis talampayensis*; [35]) and a manus that is larger and more robust than the pes (i.e., *Odontochelys*; Figure 3). Many of the osteological correlates associated with forelimb digging are similar to those for forelimb powered swimming, as both activities use the forelimb to propel the body forward by the displacement of surrounding mediums (soil versus water). However, one correlate unique to fossoriality is manual ungual phalanges that are both wider and longer (~40% longer than the penultimate phalanges) than those in non-fossorial taxa. These large claws serve an important functional role in forelimb digging, namely breaking up substrate [15], but do not aid in forelimb powered swimming. Large manual claws is a feature shared by *Eunotosaurus*, *Odontochelys*, *Proganochelys quenstedti* [36], and *Palaeochersis* (Table S2), supporting the hypothesis that fossoriality played an important role in the early evolution of turtles.

We hypothesize the correlates related to fossoriality facilitated movement of stem turtles into aquatic environments early in the evolution of the group (Middle to Late Triassic). Both gross anatomy [37] and osteohistology [38] indicate that the earliest fully shelled turtles, *Proganochelys* and *Palaeochersis*, were terrestrial. In addition, with the exception of *Odontochelys* found in near shore marine sediments [4], all other stem turtles are

Figure 3. Fossorial Osteological Correlates in the Turtle Stem

Many fossorial osteological correlates found in *Eunotosaurus* are also found in other stem turtles.

(A–C) *Odontochelys* (IVPP V 13240) retains a prominent deltopectoral crest on the humerus (A), a short, robust ulna with an ossified olecranon process (A), and hands (B, dorsal view) that are larger and more robust than the feet (C, dorsolateral view). As in most other stem turtles, the terminal manual phalanges of *Odontochelys* are large, approximately 40% longer than the penultimate phalanges.

(D–G) The hands (D, ventral view) of *Eunotosaurus* (G; FPM 2014/269) are larger and more robust than the feet (E, lateral view; F, dorsolateral view). The terminal manual phalanges (D) are large, approximately 20% longer than the penultimate phalanges.

found in continental terrestrial sediments. Interestingly, both *Pappochelys* and *Proganochelys* are found in lacustrine sediments associated with fully terrestrial animals [6, 36], whereas *Eunotosaurus* is most commonly found in terrestrial floodplain sediments associated with abundant mud cracks indicative of ephemeral bodies of water (B.S.R. and R.M.H.S., unpublished data). Combined, these data support the conclusion that the earliest known stem turtles occurred in terrestrial environments, likely associated with ponds and/or lakes, and *Odontochelys* perhaps represents an early excursion of turtles into near-shore marine environments [39]. This marine excursion was facilitated by the overlap in functional demands between forelimb digging and forelimb swimming.

The Karoo Basin of South Africa was generally semi-arid during the Middle and Late Permian becoming increasingly more arid in the Early Triassic [40], and burrowing is hypothesized [29, 41] to be a behavioral strategy commonly used by tetrapods in response to environmental stress (e.g., *Diictodon*, *Procolophon*, *Lystrosaurus*, *Thrinaxodon*, etc.). In addition, fossoriality is hypothesized to be an important factor determining which taxa survived the end-Permian mass extinction [16, 41]. We propose that the adaptations for fossoriality buffered early stem turtles from the rapid climatic drying associated with this mass extinction on land.

A fossorial stage in the early history of the turtle stem lineage provides a robust explanation for the initial stages in the evolution of the turtle shell. The current protective function of the shell appears to be an exaptation; the original expansion of the ribs was an adaptation for stiffening the skeleton to provide a stable base from which to operate a powerful forelimb digging apparatus—a functional requirement for fossorial animals. The functional advantages conferred by broadened ribs, in the context of an arid environment where fossoriality is a common survival strategy, provided the initial impetus for the origin of the turtle shell and represents a crucial stage in the evolutionary history of turtles.

EXPERIMENTAL PROCEDURES

Material Analyzed

The skeletal morphology of 47 *Eunotosaurus africanus* specimens was examined. The following specimens exhibited previously undescribed anatomical elements: USNM 23009 includes an undescribed ulna; additional preparation to M777 revealed an acromion process on the scapula; FPM 2014/269 is a mostly complete postcranial skeleton that preserves the first complete hindlimb and forelimb; and SAM-PK-K11350 preserves both sclerotic rings.

Histology

The petrographic thin sections were prepared using standard procedures [42] on an ulna (USNM 23009), humerus (CGP/1/3000), and fibula (BP/1/7024). The thin sections were analyzed using a Leica DM 2500 M composite microscope, equipped with a LEICA DFC420 C digital camera and Nikon Eclipse 50i polarizing microscope, equipped with a DS-Fi1 digital camera. Processing and preparation of images was accomplished using Adobe Photoshop and Illustrator (CS6) and CorelDraw.

SUPPLEMENTAL INFORMATION

Supplemental Information includes one figure and two tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.05.020.

AUTHOR CONTRIBUTIONS

T.R.L. designed the project. T.R.L., T.M.S., J.B.-B., R.M.H.S., and B.S.R. collected data. All authors analyzed data and contributed in preparing the manuscript.

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Supplemental Information

Fossorial Origin of the Turtle Shell

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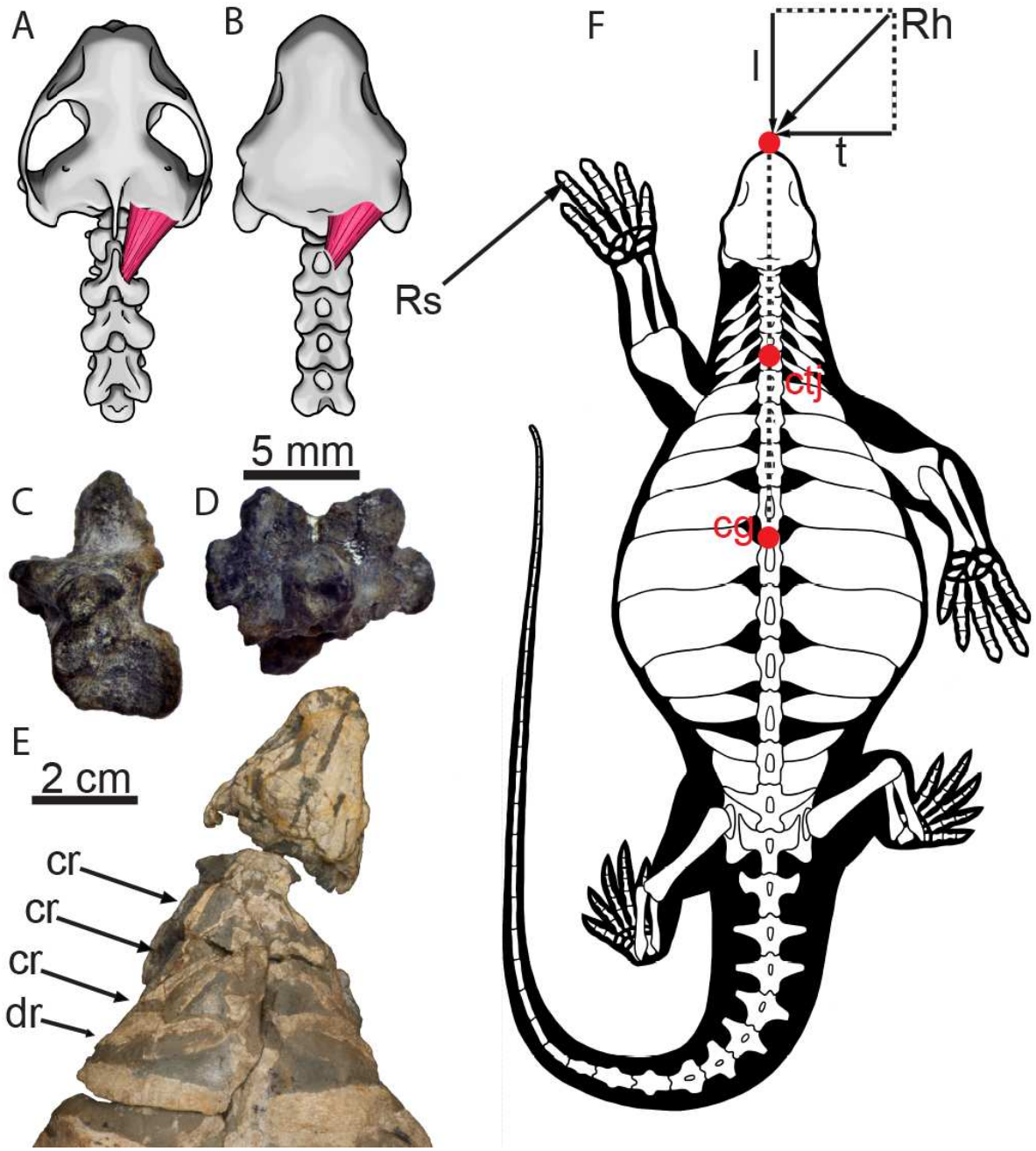

Figure S1. ***Fossoriality osteological correlates are nearly identical in*** **Eunotosaurus** ***and extant gopher tortoises (*****Gopherus*****), suggesting a similar "head bracing" method of digging for*** **Eunotosaurus, Related to Figure 2**. **A, B**, the broadened occiput of the skull in *Eunotosaurus* (**B**) and *Gopherus* (**A**), increase both the area of attachment and the mechanical advantage of neck musculature used to stabilize the cranio-cervical joint [S1] relative to amniotes ancestrally (**A**). **C, D,** the cervical vertebrae (USNM 23009 in left lateral (**C**) and dorsal (**D**) views) of *Eunotosaurus*, like those in *Gopherus*, are short and robust with bulbous neural spines and massive zygapophyses situated between the vertebral bodies, which indicate well-developed neck musculature. **E,** *Eunotosaurus* (CM777) has long, deep cervical ribs (cr) that merge with the dorsal ribs (dr) to create a fusiform body. **F**, diagrammatic dorsal view of "head

braced" forelimb digging thought to have been present in *Eunotosaurus* (modeled after that found *Gopherus* [S1]). The digging stroke of the left manus against the soil creates resistance (Rs) that acts at the manus, creating a forwardly directed translational force to the body of *Eunotosaurus*, in addition to a rotational force. The rotational force causes the body to pivot clockwise about its center of gravity (cg). The head and neck brace against the soil to oppose the rotational force and prevents the body from pivoting. This creates a resistance force against the head (Rh) and consists of a posteriorly acting longitudinal component (l) and transverse (t) component. These forces produce compression and bending within the skull, neck, and the connection of the neck with the body at the cervico-thoracic joint (ctj).

Table S1 – ***List of osteological correlates for fossoriality in sprawling and upright taxa.***

	Mode of Locomotion					
Digging Mechanism Adaptations	**Sprawling Taxa**				**Erect Taxa**	
	Eunotosaurus† stem turtle	*Gopherus* gopher tortoise	*Thrinaxodon*† stem mammal	*Myremecophaga* giant anteater	*Talpa* mole	*Taxidea* badger
distinct tubercle on posterior edge of coracoid	Present	Absent	Absent	na	na	na
acromion process on scapula	Present	Present	Present	Present	Absent	Present
distinct deltopectoral crest on humerus	Present	Present	Present	Present	Present	Present
robust humerus =/> femur	Present	Present	Absent	Absent	Present	Present
short robust ulna	Present	Present	Absent	Present	Present	Present
ossified olecranon process on ulna	Present	Present	Absent	Present	Present	Present
size of manus (M) relative to pes (P)	M>P	M>P	M=P	M>P	M>P	M>P
terminal phalanges larger than penultimate phalanges	Present	Present	Absent	Present	Present	Present
abundant Sharpey's fibers on forelimb	Present	Present	Present	?	?	?
abundant Sharpey's fibers on forelimb	Present	Present	Present	?	?	?
Counteractive Forces Adaptations						
short, spade shaped skull	Present	Present	Present	Absent	Present	Present
broadened occiput of skull	Present	Present	Present	Absent	Present	Present
short, robust cervical vertebrae	Present	Present	Present	Present	Present	Present
craniocaudally broadened dorsal ribs	Present	na	Present	Present	Absent	Absent
Sensory Adaptations						
small optical ratio/eye not sensitive to light	Present	Present	?	Absent	Present	Absent
eye size	Large	Large	?	Large	Small	Large

Table S2 – ***List of osteological correlates for fossoriality in stem and crown turtles.***

Digging Mechanism Adaptations	*Eunotosaurus†* stem turtle	*Pappochelys†* stem turtle	*Odontochelys†* stem turtle	*Proganochelys†* stem turtle	*Palaeochersis†* stem turtle	*Gopherus*
distinct tubercle on posterior edge of coracoid	Present	Absent	Abesent	Absent	Absent	Absent
acromion process on scapula	Present	Present	Present	Present	Present	Present
distinct deltopectoral crest on humerus	Present	Present	Present	Present	Present	Present
robust humerus =/> femur	Present	Present	Present	Present	Present	Present
short robust ulna	Present	?	Present	Present	Present	Present
ossified olecranon process on ulna	Large	?	Small	Small	Large	Small
size of manus (M) relative to pes (P)	M>P	?	M>P	M=P	M=P	M>P
terminal phalanges larger than penultimate phalanges	Present	?	Present	Present	Present	Present
abundant Sharpey's fibers on forelimb	Present	?	?	?	?	Present
thickened cortical bone of forelimb	Present	?	?	?	?	Present
Counteractive Forces Adaptations						
short, spade shaped skull	Present	?	Absent	Present	Present	Present
broadened occiput of skull	Present	?	Present	Present	Present	Present
short, robust cervical vertebrae	Present	?	Present	Present	Present	Present
craniocaudally broadened dorsal ribs	Present	Present	Present	Present (shell)	Present (shell)	Present (shell)
Sensory Adaptations						
small optical ratio/eye not sensitive to light	Present	?	?	?	?	Present
eye size	Large	?	?	?	?	Large

Supplemental References

[S1] Bramble, D. M. (*1982*). *Scaptochelys*: Generic revision and evolution of gopher tortoises. Copeia *4*, 852 – 867.